

# ITINERANT POLLINATORS IN A FOREST

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The familiar sight of flowers in a sunny meadow beset by a profusion of insect-visitors sharply contrasts with that of flowers inhabiting a quiet forest, apparently unvisited by flower-loving insects. Yet many plant species bear entomophilous flowers in deep shade beneath trees where there appears to be an extreme paucity of anthophilous insects. Several authors have commented upon the importance of sunlight to insect visits with the observation that shade inhibits many flower visitors (Perkins, 1919; Linsley, 1958; Free, 1960) while others will not penetrate the comparative gloom of the interior of a wood or forest (Kerner and Oliver, 1895). The presentation of entomophilous flowers by shade-loving species with such an apparently meagre chance of insect visits appeared anomalous, and worth investigation.

A shade-loving violet, *Viola glabella* Nutt., was selected for study. This species possesses delicate, deep yellow flowers 6–16 mm long. They are clearly entomophilous in common with the chasmogamous flowers of the majority of the other species in the genus. The population studied was located in the coastal redwood, *Sequoia sempervirens*, forests of the Santa Cruz mountains at an altitude of 450 ft in San Mateo Co., California.

To discover whether or not they were self-pollinating 20 flowers on the point of opening were enclosed in fine-mesh nylon bags to exclude insect-visitors. Eighteen flowers did not develop seed while 2 contained a small proportion of enlarged ovules. These results strongly suggest that selfing was uncommon and that insects were required for pollination.

Preliminary observations suggested that flower visitors were present in the forest but were confined to the pools of sunlight resulting from gaps in the canopy. Consequently, three study sites were chosen, each of approximately 1 sq m, which were known to be hit by sunshine for a short time during the day. Each site harboured at least 20 open flowers of *Viola glabella* and 1 to 5 flowers of *Oxalis oregana* and/or *Trillium chloropetalum*. Observations were continued for five days from 10:00 a.m. to 4:00 p.m. each day.

Light intensity readings were taken from a Weston Illumination Meter with the probe held level with the leaf subtending an open violet flower, see Fig. 1. A Yellow Springs Tele Thermometer with 8 probes was used to measure the temperature throughout each site. Each thermistor was secured immediately below a leaf subtending an open flower, see Fig. 1. A constant watch on insect activity was maintained (with the aid of an assistant) and all flower visits and insects counted.

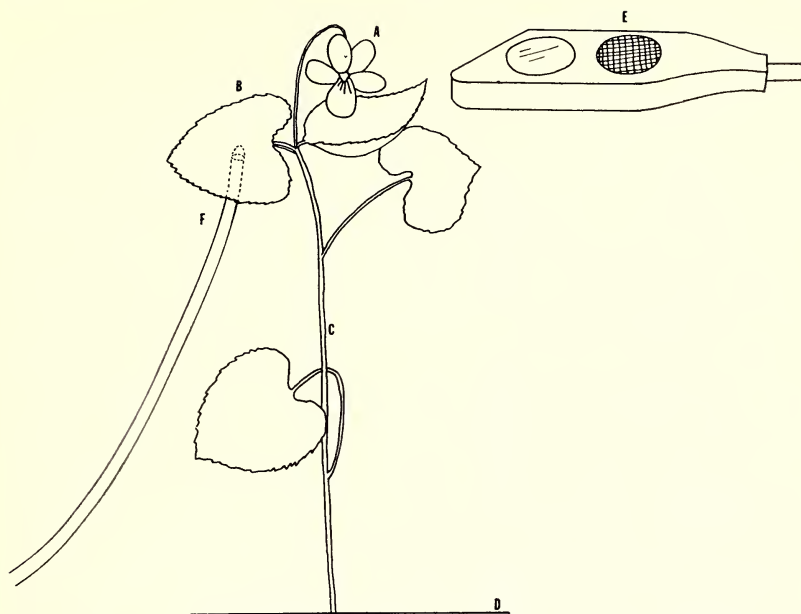


FIG. 1. Sketch to show a plant of *Viola glabella* with thermometer and lightmeter in position: A, flower; B, leaf subtending flower; C, main stem; D, ground level; E, lightmeter; F, thermometer probe.

Light intensity and temperature readings were taken at half-hour intervals throughout the day. However, these remained relatively constant except around the immediate period when direct sunlight fell on the site. Therefore, attention from now on will be focused upon the half-hour immediately before the arrival of direct sunlight at the site, the half-hour during which it was present and the half-hour immediately following its departure. During this  $1\frac{1}{2}$  hours of intensive observation readings were taken every minute. The period of direct sunlight was never longer than 15 minutes but sun specks were generally present for up to 30 minutes.

Figure 2 summarizes the findings. Temperature and light readings remained fairly constant throughout the day. With the advent of direct sunlight at the site, however, there was a dramatic increase in both over a period of 4–5 minutes. The temperature rose by approximately 5 degrees and the light intensity by up to 8000 foot candles. Whilst in shade each site received occasional visits from Muscid or Calliphorid flies, crane flies (Fam. Tipulidae) and winter crane flies (Fam. Trichoceridae). No insects present were conspicuously anthophilous and no flower visits took place. By contrast, as each site received direct sunlight, many insects would quite suddenly appear. It was astonishing how rapidly insect activity increased: Bibionid, Muscid, Calliphorid and Tachinid flies appeared, apparently to bask in the warmth. Sawflies

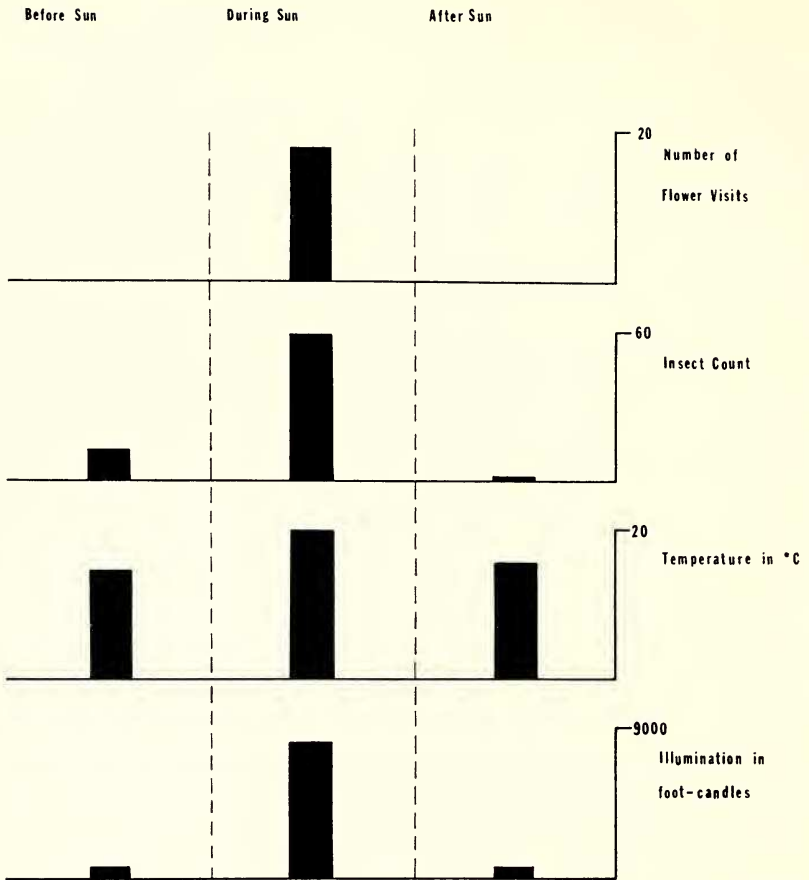


FIG. 2. Histograms to show the correlation between the number of flower visits, insect counts, the temperature and the light intensity. Each represents the average of the figures from 5 days of observation.

(Fam. Tenthredinidae), hoverflies (Fam. Syphidae), small bees (Fam. Andrenidae, Halictidae) and occasional butterflies would fly in and alight on leaves or visit flowers. It was interesting to find that shortly following the arrival of the van of insects there was often a quiet influx of a few parasitic species particularly Ichneumons, Conopids and solitary wasps. Figure 2 clearly shows that all flower visits observed took place during the 15 minutes or so when the sun shone on the site.

As the sunlight left each site the insects disappeared just as suddenly as they had appeared. A mere 5 minutes later the temperature had dropped by 4–5 degrees, the illumination by 7000–8000 ft candles and the insects had almost entirely deserted the spot. Those remaining were invariably species which moved with impunity through the forest ap-

parently indifferent to the quantity of light in their path (Tipulidae and Trichoceridae).

*Viola glabella* was visited by 3 species of hoverflies, kindly identified by Lloyd Knutson: *Sphegina infuscata* Loew, *Sphegina armatipes* Malloch and *Xylota rainerei* Shannon, and by species of solitary bees, kindly identified by G. I. Stage: *Andrena* sp. and *Lasioglossum* subgenus *Evylaeus*. I have no information on the distribution or ecology of these species but investigation of the stigmas of the flowers they visited confirmed that they were capable of pollination. *Oxalis* flowers received occasional visits from these species but *Trillium* was entirely ignored by them. The violets appeared to monopolize the attentions of flower-visitors.

The work described here was a pilot project for a much larger study of pollen exchange in a forest environment to be carried out over a period of 2 years. However, the rapid emergence of 2 important points of pollination ecology prompt this early discussion: firstly, the study has emphasized the need for caution concerning generalizations in pollination ecology. The present case, in common with a number of others, shows that a detailed investigation may reveal the situation to be more complex than was originally supposed. In the study sites the flowers of plants which inhabited deep shade were visited by efficient pollinators—including those belonging to groups more frequently thought of as sun-loving, such as hoverflies and solitary bees. A continuous watch on the habitat confirmed that pollinators were available but that they were itinerant, moving on with the progress of patches of sun. Outside of these paths of illumination flower visits may have indeed been very rare. Pollination by nocturnal or crepuscular visitors was always a possibility but the main point is that diurnal visitors were there, albeit confined to small and ephemeral patches of sunlight, and that a thorough study was required to discover this.

The pool of sun had to be sufficiently prolonged to draw anthophilous insects to the spot. This observation leads directly to a second point, previously noted by several authors but still requiring reiteration, that the immediate locality of a plant may be of prime importance in its pollination. For violets in the study sites the precise location of the plant relative to gaps in the canopy directly affected the frequency of insect visits and, therefore, the frequency of cross-pollination. The species in question produces seed by means of self-pollinated cleistogamous flowers later in the season but insect visits provide the sole opportunity for out-breeding and they are, therefore, the only agents for genetic exchange within the population. That within a small area insect visits may be confined to narrow tracts of sunlight resulting from gaps in the canopy means that only a fraction of the population may be out-breeding. In the event of change or disturbance of the environment this fraction, in providing new genetic recombitants, may be vital to the further evolution of the species.

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#### NOTES AND NEWS

THE INTRAGENERIC POSITION OF *SALIX ORESTERA*.—*Salix orestera* was described by Schneider (*J. Arnold Arbor.* 1:164. 1920) and placed in the section *Adenophyllae*. Prior to the naming of this species, specimens had been identified as *S. glauca* L. var. *villosa* (Hook.) Anderss. by such botanists as Bebb (*in* S. Watson, *Bot. Calif.*, Vol. 2, Cambridge, 1880) and Jepson (*Fl. Calif.*, Part 2, Berkeley, 1909). Later Jepson (*Manual Fl. Pl. Calif.*, Berkeley, 1923) changed *S. orestera* to a variety of *S. glauca*.

Taxonomists have not agreed on the position of *S. glauca* within the genus. Schneider (op. cit.) stated that "*Salix orestera* seems to be most closely related to *Salix eastwoodiae*." Archer (*Contrib. Fl. Nevada.* 50. 1965) combined *S. orestera* and *S. eastwoodiae* under the latter name. Argus (*Contr. Gray Herb.* 196:1-242. 1965) stated that "other species including *Salix eastwoodiae* (incl. *oresteria*) seem to be closely related to this group and further study may include them."

The three taxonomists, mentioned in the paragraph above, all have mentioned a relationship of some kind between *S. eastwoodiae* and *S. orestera*. However, these two taxa are distinct. The leaves of *S. eastwoodiae* are green on both sides, with cream-colored glands on the surfaces and margins of the blade. The leaves of *S. orestera* are green above and glaucous beneath, and glands are not present on the surfaces and margins of the blade. The relationship that exists is one of intensive hybridization and introgression between *S. orestera* and *S. eastwoodiae*. Many herbarium specimens are intermediate between these two species, and it is easy to understand why Schneider and Archer treated these two taxa as they did.

*Salix orestera* is closely related to *S. glauca* and should not be included in section *Adenophyllae*. *Salix orestera* occurs in the Sierra Nevada and San Bernardino Mountains of California, northeastern Nevada, and the Cascade Mountains of Oregon. Argus (op. cit.) listed the *S. glauca* complex as occurring in every western state including Canada except for California, Nevada, Oregon, and Washington. Thus, the distribution of *S. orestera* indicates that it should be considered a major geographical segment of *S. glauca*. After studying many specimens including the types of the taxa involved, I propose a new combination.

*SALIX GLAUCA* L. ssp. *oresteria* (Schneider) Youngberg, comb. nov. *S. orestera* Schneider, *J. Arnold Arbor.* 1:164. 1920.—ALV DAN YOUNGBERG, 5659 Rudy Drive, San Jose, California 95124.